TAXONOMY AND HETEROSTYLY OF NORTH AMERICAN GELSEMIUM (LOGANIACEAE)

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According to available floras the genus *Gelsemium* is represented in North America by two species. One is *G. rankinii* Small which occurs within 120 miles of the seacoast from North Carolina to Louisiana and the other *G. sempervirens* (L) Ait. f., which is known in the United States from Virginia to Arkansas and eastern Texas, Mexico, and Guatemala (Standley, 1924). Both species are woody evergreen vines with attractive yellow funnelform corollas. Another species occurs in eastern Asia.

Although *G. sempervirens* was known by Linneaus (1753) and to earlier authors as well (e.g., Gronovius, 1739), *G. rankinii* apparently was not recognized in literature until Nuttall (1818) referred to a variety of *Gelsemium* with inodorus flowers. Much later Small (1928) described it as a species. The description and accompanying illustrations clearly indicate the dimorphic nature of its flowers. Dimorphism in *G. sempervirens* is well illustrated by Alexander (1929). The first reference to the dimorphic nature of *Gelsemium* flowers that is known to us is that by Walter (1788). In his description of *G. sempervirens* he states, "Varietates, staminibus longioribus; stylo longiore." This may be the earliest report of heterostyly for any species. The earliest observation of heterostyly reported by Darwin (1884) is that by Persoon in 1794.

Some aspects of the dimorphism and the apparent intergradation of certain diagnostic characters prompted the present study which included extensive field research and breeding experiments as well as studies of herbarium specimens. Problems attacked included the possible correlation of certain morphological and cytological features with the species and heterostylic type involved, some genetical aspects of the heterostyly, the value of characters reported to be of diagnostic value, the distribution of the species, and the extent of any regional variation in the species. Although some questions have not been answered it is appropriate to report what has been learned.

STUDIES OF GROSS CHARACTERISTICS

According to the descriptions and keys given by Small (1933) the two species differ in several gross characteristics, i.e., those that ordinarily are used in manuals and in descriptions of species. Our observations have led to the following conclusions. The flowering shoots of *G. sempervirens* are more likely to be green and those of the *G. rankinii* red-tinged, than

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the reverse which is given by Small. The dilation of corolla tubes of the two species is so frequently similar that this character is of little use diagnostically. The body of the capsules of both species is generally veined, in *G. sempervirens* slightly more veined, this apparently being somewhat correlated with the size of the capsules. The species have nearly the same range in length of corolla and corolla tube instead of those of *G. rankinii* being clearly the shorter. The lengths of stamens and pistils in pin types, and also in thrum types of flowers, are essentially the same for both species.

Observations on many fresh flowers over a wide geographic range in the field east of Mississippi indicate that *G. sempervirens* always has odorous flowers and that *G. rankinii* usually does not. Several populations of the latter, however, have been found to have faintly to strongly odorous flowers, a condition apparently not reported in literature. In these populations the possibility of introgression with *G. sempervirens* was considered but was concluded to be improbable because features characteristic of *G. sempervirens* were mostly lacking on those plants with odorous flowers. More information about the possibility of introgression will be found later in our discussion of leaf base angles, pollen sizes, pollen fertility, and chromosomal studies.

Leaf bases in *G. sempervirens* are reported by Small (1933) to be narrowed at the base and those of *G. rankinii* rounded. Our data show that this is only generally true and that the species often cannot be separated by angles of the leaf bases. Angles were measured from special collections from the field and supplemented by others from herbarium specimens. The widest angle and the narrowest angle encountered on each collection were recorded. The maximum angle of the leaf bases for *G. sempervirens* was from 70° to 150° and for *G. rankinii* from 110° to 180°. The minimum angles were from 40° to 100° and 80° to 160° respectively. Those collections of *G. sempervirens* with any leaf base over 110° were examined for other characters typical of *G. rankinii*. None was found, the other characters definitely being those of *G. sempervirens*. In the case of those collections of *G. rankinii* having a maximum leaf base angle under 150° examination was made for other characteristics of *G. sempervirens*. None was found except that three collections with angles of 120°, 130°, and 135°, respectively, had odorous flowers. This is of no great significance, however, for there are more collections of otherwise typical *G. rankinii* having as small or smaller angles of the leaf base and there were five odorous flowered collections having larger angles (to 180°).

Leaf length and width for the two species were also studied. Data from over a hundred leaves of each species when averaged, plotted in a scatter diagram, and otherwise analyzed, show that the leaves of *G. sempervirens* average less in width and more in length, but only generally have a larger length-width ratio than those of *G. rankinii*.

Ratios for the former were from 2.9 to 5.1 and for the latter 1.0 to 3.9.

Observations were made in the field during anthesis on the colors of the corollas of fresh flowers of the two species. The two species could often be distinguished on this basis, the colors of the flowers of *G. rankinii* usually being the darker. The colors for *G. sempervirens* were: brilliant yellow (2.5Y-9/9 of the Nickerson Color Fan, published by the Munsell Color Co., 1957) to moderate orange yellow (10YR-8/10). For *G. rankinii* they were: vivid yellow (2.5Y-8/12) to strong orange yellow (7.5YR-7/11). The inner part of the corolla tube of both species, and especially of *G. rankinii*, was darker than the remainder of the corolla.

On the basis of the characters discussed above many herbarium specimens or plants in the field, especially those without flowers or fruits, would be difficult to place to a taxon. There also might be some doubt about maintaining two species. Such doubt is dispelled by other gross characters, these of the flower and fruit. The sepals, which appear not to be united, are obtuse to broadly pointed in *G. sempervirens* and acute to usually acuminate in *G. rankinii*. Pedicels in the former are scaly throughout (an occasional one may be partially naked), whereas in the latter the upper part of the pedicel is naked (an occasional pedicel will have a single scale reaching the base of the calyx, this being less frequent for fruits and mature flowers than for flowers just having opened). The body of the mature fruit of the former is 14.0 to 23.0 mm long and 8.0 to 11.0 mm wide, the beak being 1.3 to 3.0 (5.4) mm long. For the latter the data are 9.0 to 12.5 mm, 5.5 to 8.0 mm, and (2.4) 3.0 to 4.3 mm, respectively. Beak measurements for *G. rankinii* under 3.0 mm were fruits of the previous year, the shortness apparently being due to disintegration during the winter. For *G. sempervirens* measurements over 3.0 mm are uncommon and include a part or all of the upper portion of the style. This portion apparently falls off later as a unit, for beaks were either under 3.1 mm or over 5 mm long. In the latter case a region of dehiscense was usually evident. The seeds readily distinguish the two species for those of *G. sempervirens* are winged and those of *G. rankinii* not.

The possibility of correlation of pin and thrum flower types with gross characters was also studied. The characters included length of corolla and corolla tube, color of corolla, leaf dimensions, and fruit dimensions. No correlation was found.

DISTRIBUTIONAL STUDIES

Observations in the field and data accompanying herbarium specimens show that *G. rankinii* grows in moist to wet situations and is confined to the Coastal Plain of the southeastern United States (Fig. 1). Although *G. sempervirens* occasionally occurs in moist situations, it only rarely grows in wet habitats. In the southern United States it is found abundantly in drier situations, including shallow soils of granite outcrops and being associated with scrub oak vegetation of sandhills as far inland

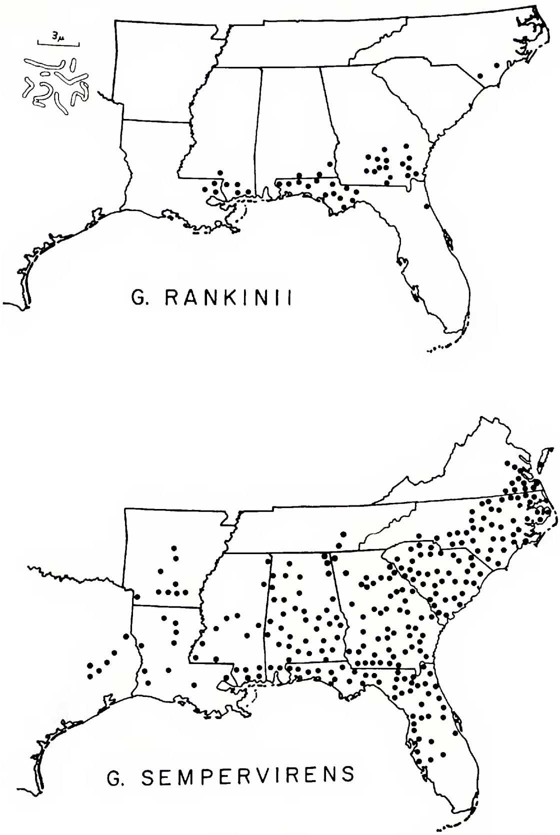

Fig. 1. TOP. Distribution of *Gelsemium rankinii* as indicated by herbarium specimens. Insert: Drawings of somatic metaphase chromosomes in a root cell of *G. rankinii*. BOTTOM. Distribution of *G. sempervirens* as indicated by herbarium specimens.

as the Fall Line. This species has a much wider geographic distribution than the former. The known distribution except for Mexico and Guatemala is also given in Fig. 1. Records for Alabama and Virginia include those reported by Harper (1928) and Massey (1961), respectively. *G. sempervirens* has been reported for Oklahoma by Vines (1960). We made no special effort to locate specimens to authenticate this report, but *Gelsemium* is not included in Waterfall's (1960) flora of Oklahoma. We believe, therefore, that the genus does not occur in that state. Coulter (1891) includes this species in his Botany of West Texas (west of 97th meridian), but we find no specimens to verify its occurrence in that region. Data from Standley (1924) and Martinez (1959) place *G. sempervirens* in Mexico (states of Chiapas, Oaxaca, Puebla, Veracruz) and Guatemala. The northernmost station appears to be Hanover Co., Virginia.

EPIDERMAL STUDIES

Microscopic studies were made of the lower epidermis of the two species by using herbarium mounting plastic in a technique very similar to that described by Sinclair and Dunn (1961) in their method A. The number of stomates per .0926 sq mm varied from 20 to 34 in *G. sempervirens* and 34 to 46 in *G. rankinii*. These data were based on the average of two counts made from peels from a leaf from each of twenty specimens of each species. Stomatal size was evaluated by measuring ten imprints on a plastic peel from a leaf from each of twenty specimens of each species. Distances measured for length and width values were between the ends of the guard cells and between their distant sides. These data are presented in Fig. 2, a scatter diagram. It is obvious that the measurements of stomates of *G. sempervirens* are usually the larger. There was no significant difference in respect to measurements of size and density of stomates between plants bearing pin and thrum type flowers.

Larger stomatal size and a lesser number of stomates per unit of area have been shown by Celarier and Mehra (1958), Stone (1961), and others to be associated with a higher degree of polyploidy when comparing species of a given genus. Our guard cell data, therefore, suggest that *G. rankinii* has a lesser number of chromosomes than *G. sempervirens*.

The surface of the lower epidermis, much more abundantly in *G. rankinii* than *G. sempervirens*, appears to be finely grooved in lines oriented along the sides of the stomates. These lines and other features of the epidermis need further studies which should include cross sections of leaves.

STUDIES OF POLLEN

The sizes of pollen grains have been known to differ in pin and thrum types of flowers at least since Darwin's (1862) studies of dimorphism in *Primula*. Also, larger sizes of pollen grains have been shown by many to be associated frequently, although not invariably, with a higher degree

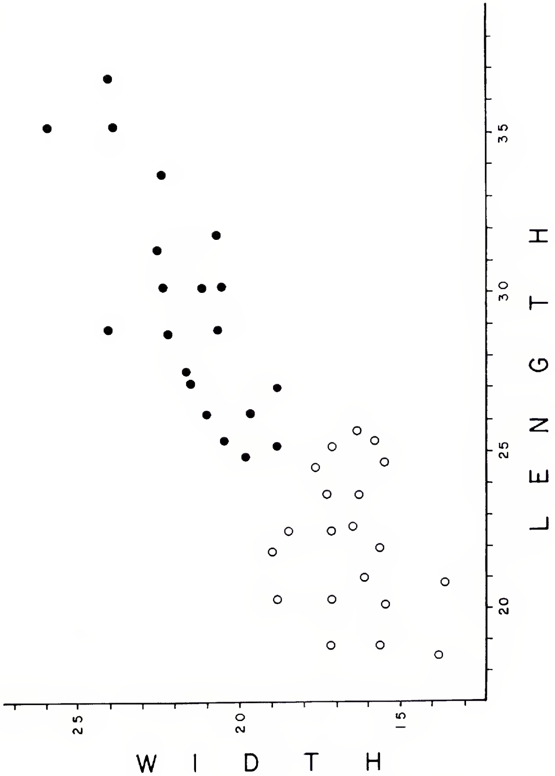

Fig. 2. Scatter diagram of measurements of stomatal size in *Gelsemium rankinii* (circles) and *G. sempervirens* (dots).

of polyploidy. A recent study describing such a situation is that of Stone (1963) in a study of *Carya* species. A study of pollen sizes in *Gelsemium*, therefore, seemed desirable.

The pollen studied was obtained from dried specimens from herbaria and supplemented by specimens collected for this purpose in the field and dried in presses over electric driers along with other herbarium specimens. A single anther was removed from a flower of each collection to be studied, dissected in water, and then observed under a microscope at 430X. The diameters of ten apparently normal pollen grains were recorded for each collection.

The data obtained on pollen size are summarized in Table 1.

TABLE 1. *AVERAGE POLLEN SIZES*[a]

Flower Type	*G. rankinii*	*G. sempervirens*
Pin		
No. of samples	21	30
Minimum	31.3	34.0
Maximum	36.7	42.2
Mean	34.3	38.1
Thrum		
No. of samples	20	29
Minimum	34.4	35.7
Maximum	43.9	45.6
Mean	40.8	41.5

[a] Expressed as diameter in microns. Based on measurements of ten pollen grains from each collection.

It may be seen that the average diameter measurements of pollen of thrum type flowers are larger than those of pin type, a situation reported by Ray and Chisaki (1957) for two species of *Amsinckia*, Translating the measurements into volume of the pollen, that of the thrum would be 67% larger than that of the pin in *G. rankinii* and 29% in *G. sempervirens*. These volume differences between thrum and pin types might be associated with the different distances the derived pollen tubes would need to grow to allow fertilization of the eggs.

A comparison of average measurements of pollen for the two species (Table 1) shows that they are larger for *G. sempervirens* in both the pin and the thrum types of flower. Pollen size data, therefore, as well as stomatal size and density, indicate a lower number of chromosomes for *G. rankinii*.

Shape differences in pollen grains also have been known to be associated with heterostyly, e.g., Johnston (1952). In both species of *Gelsemium* the pollens seemed to be of uniform size except for shrunken grains. Counts were made of the number of these per hundred grains. The numbers varied from 0 to 70 and were not associated with style type. Since shrunken grains are indicative of abortion and abortion is often present in hybrids, we investigated the possibility of relation of the numbers of such grains to possible hybridization between the two species. The specimen with 70% "aborted" pollen was of *G. sempervirens*. Although this was from a locality only a few miles from where *G. rankinii* was known to grow, the specimen exhibited no other evidences of hybridization between the two species. It was also noted that relatively high percentages of "aborted" pollen were frequently found on specimens of *G. sempervirens* that were from localities a hundred miles or more from where *G. rankinii* is known to occur. The evidence from our pollen studies, therefore, does not indicate that hybridization occurs between the two species.

PHENOLOGICAL STUDIES

There is evidence that the flowering periods of the two species of *Gelsemium* differ. Small (1928) stated that Mr. H. A. Rankin wrote that in the vicinity of Hallsboro, N. C., *G. rankinii* bloomed 20 days later than *G. sempervirens*. On 30 Mar. 1963 in Echols and nearby counties in Georgia the senior author observed the latter species to be nearly past flowering while the former was just approaching maximum flowering. During the Spring of 1964 *G. rankinii* plants transplanted to the senior author's premises did not begin to blossom until after those of the other species planted there had ceased flowering.

When data from herbarium specimens throughout the entire range of both species were analyzed no appreciable difference in flowering time was discernable. When data were confined to specimens from areas where both species occur (omitting the small disjunct area in North Carolina), it was found that the Spring flowering period of *G. sempervirens* was from 1 Feb. to 1 Apr. and *G. rankinii* essentially from 16 Feb. to 19 Apr. One specimen of the latter species in flower on 29 Jan. was collected about 10 miles south of St. Augustine, St. Johns Co., Fla. This early flowering date may be associated with the close proximity of the plants to the ocean. Both species occasionally flowered in October and there is one record for *G. rankinii* on 27 Sept. A plant of *G. sempervirens* brought in from the woods nearby and cultivated in Chapel Hill, N. C. is recorded (specimen No. 31472 in U.N.C. Herbarium) as blooming every Fall, almost as abundantly as in the Spring. Herbarium records indicate that from 30° 30′ southward, flowering of *G. sempervirens* begins 1 Feb. and is essentially completed by 1 Apr. In the Coastal Plain of Ga. and Ala. the period is from 19 Feb. through 14 Apr. In S. C., N. C., and Va. and in the Piedmont of Ga. and Ala. flowering occured almost entirely between 16 Mar. and 1 May.

Attention was also given to the possibility of differences in flowering time between pin and thrum types of flowers. Field observations and analysis of data on herbarium specimens gave no evidence of any difference in the flowering time of these two types.

GENETICAL STUDIES

Several years ago plants of *G. sempervirens* from two widely separated colonies in Clarke Co. and from one colony in Oglethorpe Co., Georgia were transplanted for observation to the senior author's premises east of Athens, Georgia. Plants from all three colonies grew in close proximity and have flowered yearly since 1955. All had pin type flowers. No other *Gelsemium* plants are known nearer than four miles. None of the plants planted east of Athens produced fruits for eight years. On 1 April 1963 pollen from thrum type flowers was placed on the stigmas of about 50 pin type flowers of these plants. That Fall many more than 50 fruits were harvested, several of these from plants whose flowers had received no introducd pollen from the hands of the senior author. Presumably insects had carried the introduced thrum type pollen from stigma to stigma. No artificial pollinations were attempted during 1964 and again no fruits developed.

Also on 1 April 1963 branches bearing thrum type flowers in a colony of *G. sempervirens* south of Athens were carefully pruned of all opened flowers and developing fruits and enclosed in plastic bags. On the following day bags were removed and opened flowers were tagged and treated as follows: five were self pollinated, and ten received pollen from pin flowers of the isolated plants east of Athens. The bags were replaced and left on the branches until the corollas of the pollinated flowers had dropped off. That Fall six fruits had developed on flowers that had received pollen from pin type flowers and no fruits on the self-pollinated thrum type flowers.

We believe that the above data indicate that pin type plants of *G. sempervirens* are self sterile in nature and cross fertile to pollen from thrum type flowers, and possibly that thrum type flowers are self sterile and cross fertile. The latter two conclusions need to be checked by further experiments. The senior author plans to grow progeny of the isolated plants that had received pollen from the thrum type flowers in order to determine ratios of the F_1 generation for that cross. It is hoped to make additional reciprocal crosses and successful selfing experiments in order to determine the genetics of heterostyly in the two species of *Gelsemium*.

Some studies were also made of the ratio in nature of plants bearing pin and thrum type flowers. Several large population samples taken in limited areas gave quite varied results, the flowers sometimes being largely of one type or the other. Since *Gelsemium* reproduces abundantly vegetatively, a sampling was made in the field at broader intervals. No sample was taken nearer than a mile to another. They were made 27-30 March 1963 from McDuffie and Baldwin Cos., Ga. south to Duval and Suwanee Cos., Fla. For *G. sempervirens* there were 34 pin type and 38 thrum type flowers and for *G. rankinii* 10 pin and 9 thrum type. These indicate a 1:1 ratio.

Counts from herbarium specimens strongly indicate the same ratio. Specimens borrowed from other herbaria were utilized and all duplicates eliminated. All flowering specimens of *G. rankinii* were tabulated as to type. The results were 21 pin and 20 thrum type (see Table 1). Counts from herbarium specimens of *G. sempervirens* gave 111 pin and 108 thrum type. Nine pin type specimens were omitted from the above number. They were the nine available collections from Orange Co., N. C., all of which had pin type corollas. After studying the accompanying herbarium labels and discussing the data with someone familiar with the localities involved, we concluded that all nine specimens were most likely propagated from the same clone.

As has been pointed out by Crosby (1949), Ray and Chisaki (1957), and others, a 1:1 ratio, or close to it, indicates self sterility of pin and thrum type flowers and an entirely outcrossing population. Our studies of ratios, therefore, confirm the conclusions of our breeding studies that both pin and thrum type flowers are self sterile and are cross fertile.

CHROMOSOMAL STUDIES

A chromosome number of $2n=16$ has been reported for *G. sempervirens* by Moore (1947). After vain attempts to repeat Moore's method using leaf tips, root tips were taken of rooting sections of stems and the $2n$ number of 16 was verified for this species by using a Feulgen squash method.

The chromosome number for *G. rankinii* is unreported in literature. The Feulgen squash method was tried with inconclusive results on root tips from roots of layered stems of this species. It was, however, determined that active mitotic division occurred about 11:00 P.M. At this point in the studies we turned to cross sectioned root tips. Root tips were placed in a modification of Navashin's Fluid Fixitive described by Sass (1958), sectioned, stained by a modification of Newton's Gentian Violet-Iodine method described by Johansen (1940), and mounted in balsam.

From root tip material collected during the latter part of June, 1964, mitotic metaphase counts of $2n=8$ were obtained. A voucher specimen (Duncan 22020) is on deposit in the University of Georgia Herbarium (sheet No. 74279). A sample chromosome plate is shown in the inset of Fig. 1. The chromosomes are approximately 1 to 3 μ in length. Occasionally cells with approximately 16 (in the outer three rows of root cells) and rarely with 9 or 10 chromosomes were seen. Moore (1947) reported for *G. sempervirens* chromosomes 1.3-3 μ in length and occasional polyploid cells and cells with intermediate numbers in leaf smears.

Indications from stomatal and pollen data presented earlier that *G. rankinii* had a smaller number of chromosomes are thus confirmed by the determination of a $2n$ number of 8.

CONCLUSION

Our studies show that there are two distinct species of *Gelsemium* in North America and that there is probably no introgression between them. Hybrids were not detected and should not be expected in abundance since one species is diploid and the other is tetraploid.

The determination of the chromosome number of $2n=8$ for *G. rankinii* lowers the known n numbers for the Longaniaceae and the basic number for *Gelsemium* to 4. Darlington and Wylie (1955) had reported the basic number for *Gelsemium* as 8. Moore (1947) had previously cited a report of $n=6$ for two species of *Fagraea* which belongs to the same subfamily as *Gelsemium*. He suggested on the basis of cytological evidence that *Gelsemium* might have a genetic link with one branch of the Apocynaceae which are characterized by a haploid number of 8. Moore also suggested that *Gelsemium* may have diverged from an ancient line which produced the Apocynaceae. The basic chromosome number of 4 for *Gelsemium* seems to support Moore's suggestion that divergence may have occurred at such a distant time that *Gelsemium* can not be regarded, on morphological grounds, as a true member of the Apocynaceae.

Our cytological evidence indicates that *G. sempervirens* was derived more recently and probably from *G. rankinii*. Distributional data in the southern United States also indicate such a relationship. *G. rankinii* is confined to wet habitats of a limited area of the Coastal Plain (Fig. 1), while *G. sempervirens*, being a tetraploid and probably more vigorous, occurs in a variety of habitats (wet to very dry) and occupies a much wider area (Fig. 2). The reported occurrence of *G. sempervirens* in the disjunct Mexican-Guatemalan region and the apparent absence of *G. rankinii* from there could be taken to indicate that the former species is the ancestral one. Before serious conclusions involving distributions in the Mexican-Guatemalan region are made, however, the identity of all collections of *Gelsemium* from there should be checked and the absence of *G. rankinii* verified by additional studies. Most persons dealing with the flora of that region are probably unfamiliar with *G. rankinii*.

Although pin type plants are generally heterozygous and the thrum type homozygous recessive (Ray and Chisaki, 1957; et al.), we have no evidence that this is the case in *Gelsemium*. Additional breeding experiments are needed to determine the genetic makeup of the two forms as well as the extent of self sterility, especially for thrum type plants.

Our studies also have added to those known situations in which stomatal size and density, and size of pollen are correlated with ploidal levels.

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